Net CO_2 uptake rates for *wheat* (*Triticum aestivum* L.) under Cukurova field conditions: Salinity influence and a novel method for analyzing effect of global warming on agricultural productivity

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Abstract

Net CO_2 uptake rates (P_N) were measured under relatively moderate climatic conditions in Cukurove basin Turkey.The higher temperatures and lower relative humidity in the field led to a rapid response to salinity. The upper envelopes of scatter diagrams for P_N *versus* temperature which indicate the maximal rates at a particular temperature, were determined . As leaf temperature increased above 10 °C, for wheat under saline conditions (near Karatash on the easterm mediterranean) the maximal P_N increased exponentially, reaching maxima of 12 µmol m^{-2} s^{-1}near 24 °C. For wheat under more favourable conditions near Adana Turkey, as leaf temperature increased above 5 °C, the maximal P_N increased exponentially, reaching maxima of 26 µmol m^{-2} s^{-1} also near 24 °C. Based on the Arrhenius equation, the apparent activation energies of enzymatic metabolism were 118 and 240 kJ mol^{-1}, for wheat under favourable and saline conditions respectively. These values are within the range determined for a diverse group of species using different methodologies. Above the temperature of maximal P_N it decreased by an average of 55 % per 1.00 °C for the two cases. Such steep declines with temperature indicate that irrigation then may lead to only small enhancements in net CO_2 uptake ability. Global warming with only several fractions of a degree mat therefore be associated signifcant yield reduction.

Additional key words: activation energy; optimal temperature;

Introduction

Little is known about P_N under conventional cultivation conditions. Based largely on studies with conventional C_3 and C_4 crops, wheat in Turkey and elswhere is rainfedded

But how rapidly P_N decreases salinity and global warming has not been determined in the field. Thus one objective of the present study was to determine the effect of water stress under saline environment on P_N for *wheat* Another objective was to continuously monitor P_N and to measure the rates and to determine their temperature dependence under field conditions.

A technique based on the upper envelopes of the data was used to determine the maximal P_N at various temperatures, even when other factors, such as water stress or irradiance, would concomitantly limit net CO_2 uptake. Based on this technique, the apparent activation energies were determined for positive net CO_2 uptake. Above the optimal temperatures, the upper envelopes were used to characterize the inhibition of P_N by increasing temperature (Yurista 1999, Bernacchi *et al.* 2002). Enzyme activation energies are usually estimated using an Arrhenius plot (Nobel 2005) when temperature is the only independent variableunder controlled laboratory conditions (Cornish-Bowden 1995, Gutfreund 1995). Laboratory results may not always

correctly predict enzyme activity under natural conditions when multiple environmental variables are changing simultaneously. Indeed, optimal temperatures for enzymes activities are rarely determined under field conditions. The uniqueness of the data presented here are that (*1*) they were obtained under field conditions, and (*2*) they were collected for two water stress conditions for which little is known concerning the activity of the enzymes involved.

Materials and methods

Experiments on mature wheat were conducted in the Cukurova basin in Turkey from April 9 through April 19th 2005. Two fields conditions are presented in this paper Saline (about 3 dS/m) and non-saline (about 1dS/m). The average daily temperature was 16-17 °C (maximum 28 °C, minimum 9 °C). The average relative humidity was 72 % (maximum 95 %, minimum 37 %).

P_N was measured with a *PTM48* portable photosynthesis system (*PhyTech*, Rehovot, Israel). The automated system has a chamber that is closed for 2 min and then open for 28 min, when undisturbed gas exchange occurs between the stem and the atmosphere. Accessories included a *TIR-4* sensor for photosynthetic photon flux (PPF; 400–700 nm), *ATH-2* temperature and humidity sensors (all manufactured by *PhyTech*), and two 1.0-mm-diameter, copper-constantan thermocouples inserted 1.5 mm into a leaf.

The impact of temperature on P_N was analyzed for day time hours. A scatter diagram of all the positive uptake rates was determined. The upper envelope, when factors other than temperature (such as irradiance, relative humidity, soil water content, and chemical substrate amounts) would not be limiting net CO_2 uptake, was then fitted for the rising portion of the curve using an exponential based on the Arrhenius equation (Nobel 2005):

$$\text{Rate}=Be^{-A/RT} \quad (1)$$

where B is a constant, A is the apparent activation energy [kJ mol^{-1}], R is the gas constant (8.314 J mol^{-1} K^{-1}), and T is the absolute temperature [K]. Using an Arrhenius plot [$\ln P_N$ *vs.* $1/T$], A, which represents the minimum energy for the reaction, was estimated for both conditions.

Above the optimum temperature, P_N values declined with increasing temperature, presumably representing inactivation (or deactivation; Bernacchi *et al.* 2002, Sharkey 2005) of the catalytic properties of the enzymes involved. The decline in rate with increasing temperature was assumed to be proportional to the rate:

$$d(\text{Rate})/dT=-C\times\text{Rate} \quad (2)$$

where C represents the relative fraction of inactivated molecules per unit increase in temperature. Reorganizing Eq. 2 and integrating leads to:

$$\text{Rate}=De^{-CT} \quad (3)$$

where D is a constant of integration that incorporates the particular units used. Eq. 3 was used to fit the upper envelopes of P_N above the optimal temperatures.

Results

PPF reached a maximum near midday (Fig. 1) and leaf temperature reached a maximum near mid-afternoon for both saline and non saline conditions. $P_N$were maximal before midday and were generally higher for non saline than forsaline conditions.

Water stress due to salinity decreased the rates and the daily amounts of net CO_2 uptake (Fig. 2). For *non saline conditions* the maximal P_N was 25 and only about 12 μmol m^{-2} s^{-1} for the saline case .

Rates tended to rise as the temperature was raised above 5-10 °C, achieved a maximum near 24 °C, and then decreased to zero near 30 °C. Over the same temperature range, P_N

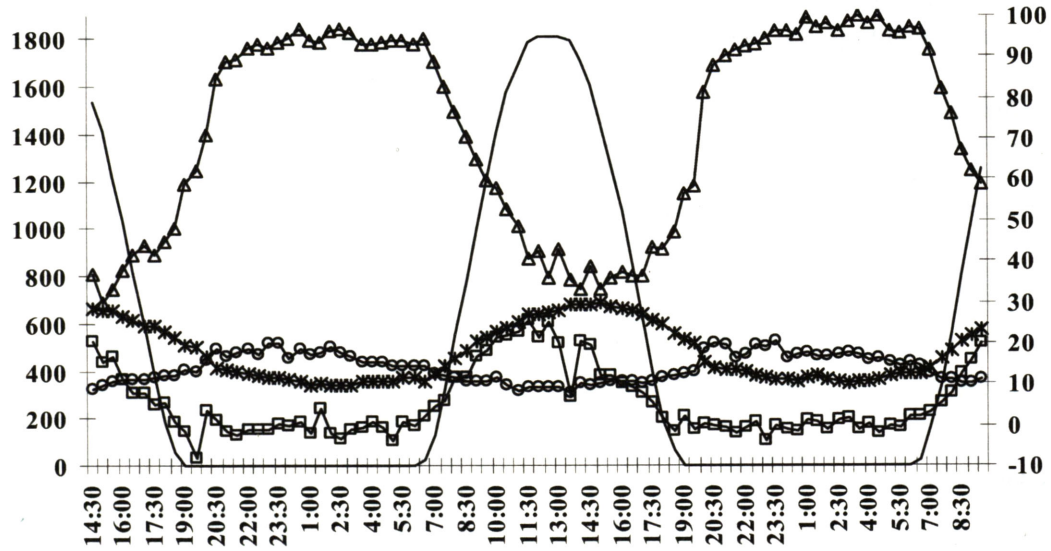

Fig. 1. Diurnal patterns of leaf net photosynthetic rate (P_N, □), photosynthetically active radiation (PAR, –), air temperature (T, ∗), relative humidity (RH, △), and atmospheric CO_2 concentration (C_{atm}, ○) measured at a wheat field of the experimental station of the Department of Agricultural Structures and Irrigation of the Çukurova University in the north on April 9 to 11, 2005.

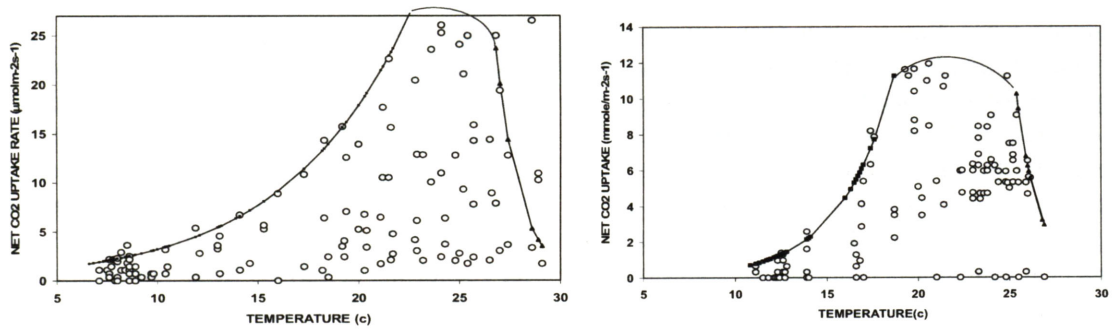

Fig.2. Temperature dependence of the net CO_2 uptake rate, P_N for salin conditions (right) andnon saline conditions (left): Data were obtained at 30 min intervals under various temperatures and degrees of water stress; The envelopes for the rising portions were analyzed using Arrhenius equation, and the envelopes for the falling portions were analyzed using enzymes inactivation equation ; parameter values are summarized in Table 1.

Parameterization of the upper envelopes (Table 1) from 10 to 24 °C indicated an activation energy (A, Eq. 1) of 118 kJ mol^{-1} for P_N in non saline case and almost double for the saline case. Parameter B (Eq. 1), which indicates the P_N for the unrealistic case of zero A, was also larger for the saline case than for non-saline conditions (Table 1). The decline in P_N above the optimal temperature was characterized by parameter C (Eqs. 2 and 3), which was the same for both conditions, (Table 1).

Table 1. Parameters for equations describing the upper envelopes of the responses of net CO_2 uptake to temperature for saline and non-saline conditions. Rising portions (below the optimal temperature) were described by Eq. 1 and falling portions (above the optimal temperature) were described by Eq. 3.

Conditions	*A*	ln *B*	*C*	ln *D*
	[kJ mol^{-1}]		[K]	
Saline (3dS/m)	240	101.7	0.83	250
Non saline (1dS/m)	118.4	51.2	0.83	252

Discussion

Salinity greatly affected P_N as wheat responded strongly to the field conditions. The maximal rate of CO_2 uptake decreased about 50 % under saline conditions.

The large number of data points for positive P_N at various temperatures (over 45) together with their inherent great scatter enabled upper envelopes to be created. Such envelopes indicate when factors other than temperature are not limiting P_N. In particular, for both saline and non-saline conditions, the maximal P_N increased as the temperature increased from about 10 to 24 °C. The maximal rate of 26 μmol m^{-2} s^{-1} for the non-saline field is very high indicating that the plants were under excellent conditions; such data have apparently not been previously reported. Based on the Arrhenius equation, the increases in P_N with temperature reflect increases in the number of molecules that have sufficient energy to surmount the energy barriers represented by the underlying reactions (Eq. 1; Nobel 2005). Above the optimal temperature, P_N decreased and became effectively zero by 30 °C. Such decreases reflect thermal disruption of the catalytic properties of the enzymes involved, or "deactivation" (Bernacchi *et al.* 2002, Sharkey 2005). Thus, if climate change is expected to increas temperature even by several tens of a degree, the effect on reduction of productivity may end up to be very significant.

Moreover,from the analysis of the envelope of P_N as the canopy temperature increased from 10 °C to the optimal value of 24 °C, the apparent activation energy (see Eq. 1) was 118.4 kJ mol^{-1} for non-saline conditions and 240 kJ mol^{-1} for saline conditions. These values of *A* are higher than CAM plants, *e.g.* 38–96 kJ mol^{-1} for nine species determined by micro-calorimetry (Feng *et al.* 1994), and within the range of the non-saline conditions for C_4 plants, *e.g.* 69–194 kJ mol^{-1} for *Flaveria bidentis* at various temperatures (Kubien *et al.* 2003). These values of *A* are higher than values of 51–69 kJ mol^{-1} for RuBPCO from ten C_3 species, 50–68 kJ mol^{-1} for seven C_4 species (Sage 2002), 59–85 kJ mol^{-1} for leaves of *Spinacia oleracea* with various temperature treatments (Lixiong *et al.* 2002), and 56–101 for *F. bidentis* at various temperatures (Kubien *et al.* 2003). Therefore, assuming that the major enzymes involved in photosynthesis are PEPC and RuBPCO the activation energies for in the field determined using the upper envelopes of the responses of net CO_2 uptake to temperature are within the range of literature values measured in the laboratory for these enzymes with various methodologies and a diverse group of species. However wheat under saline conditions required higher energy of activation before the production process starts.

Temperatures above those optimal for P_N can inactivate enzymes *via* various cellular processes as well as can influence stomatal responses (Nobel 2005, Sharkey

2005). Such inhibition, deduced from the upper envelope of the data points, was empirically represented by an exponential decay with temperature that was quantified by the relative fractional inhibition per K unit or, equivalently, per °C (C in Eqs. 2 and 3). Although C is empirical, it clearly describes the large inhibition of net CO_2 uptake with increasing temperature for these two field conditions in a temperature range that they encounter under field conditions. For example, a C of 1.00 indicates that P_N will decrease by 63 % per °C beginning at 24°C, and a C of 0.3 indicates a decrease of 26 % per °C also beginning at 24 °C. In this study C of 0.86 is somewhere between these two extrems indicating a production decease of about 55% per 1 °C above the optimal temperature. Information on the relative proportion of the inhibition due to enzyme inactivation (deactivation) *versus* stomatal and other factors awaits future research. In any case, the steep decline in P_N with temperature above 24 °C for these wheat species means that small increases in ambient temperature can then lead to significant decreases in net CO_2 uptake ability and it indicate that irrigation then may lead to only small enhancements in net CO_2 uptake.

References

Bernacchi, C.J., Portis, A.R., Nakano, H., Caemmerer, S. von, Long, S.P.: Temperature response of mesophyll conductance. Implications for the determination of Rubisco enzyme kinetics and for limitations to photosynthesis in vivo. – Plant Physiol. **130**: 1992-1998, 2002.

Cornish-Bowden, A.: Fundamentals of Enzyme Kinetics. 2nd Ed. – Portland Press, London 1995. Feng, W., Ning, L., Daley, L.S., Moreno, Y., Azarenko, A., Criddle, R.S.: Determination of effective temperature minima for CAM carboxylation in diverse plants by scanning microcalorimetry. – Plant Physiol. Biochem. **32**: 319-330, 1994.

Gutfreund, H.: Kinetics for the Life Sciences. – Cambridge University Press, Cambridge 1995.

Kubien, D.S., Caemmerer, S. von, Furbank, R.T., Sage, R.F.: C_4 photosynthesis at low temperature. A study using transgenic plants with reduced amounts of Rubisco. – Plant Physiol. **132**: 1577-1585, 2003.

Lixiong, H., Nada, K., Kasukabe, Y., Tachibana, S.: Enhanced susceptibility of photosynthesis to low-temperature photoinhibition due to interruption of chill-induced increase of S-adenosylmethionine decarboxylase activity in leaves of spinach (*Spinacia oleracea* L.). – Plant Cell Physiol. **43**: 196-206, 2002.

Nobel, P.S.: Environmental Biology of Agaves and Cacti. – Cambridge University Press, New York 1988.

Nobel, P.S.: Physicochemical and Environmental Plant Physiology, 3rd ed. – Elsevier/Academic Press, Burlington MA, 2005.

Sharkey, T.D.: Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. – Plant Cell Environ. **28**: 269-277, 2005.

Yurista, P.M.: A model for temperature correction of size-specific respiration in *Bothotrepes cederstroemi* and *Daphnia middendorffiana*. – J. Plankton Res. **21**: 721-734, 1999.

Acknowledgements

Financial support was provided by the GLOWA - Jordan River Project funded by the German Ministry of Science and Education (BMBF), in collaboration with the Israeli Ministry of Science and Technology (MOST) and the Impact of Climate Change on Agriculture Productivity (ICCAP) project in the Research Institute for Humanity and Nature (RIHN), Kyoto, Japan.